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Habitat selection of carabid beetle in deciduous woodlands of southern Belgium

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Summary. Samples of carabid beetles were collected monthly between April and October 1986 in 68 deciduous woodlands selected on the basis of their vegetation composition and their geographical locality. Habitat selection patterns of the woodland carabid fauna were determined by a two-step procedure: (1) multivariate analysis of species abundance in each sampling site and (2) measurement of relations between carabid abundance and environmental descriptors. Results show the main influences on woodland carabid distribution to be soil water holding capacity, soil trophic status and soil acidity. Carabid abundance is also related to the vegetation. The two-step procedure allows the detection of habitat selection patterns at the community level. It emphazises the need of ecophysiological studies to relate these patterns to relevant biological processes.

Key words: Carabid beetles, deciduous woodland, habitat selection, species communities, multivariate analysis

Introduction

Studies on habitat selection aim to identify the environmental factors that determine species' habitat preferences. The main synthesis on habitat selection in carabid beetles (Thiele 1977) combined both laboratory and field data to work out such specific environmental requirements. This approach suffers a major drawback: the laboratory data are based on preference experiments in which only one single environmental factor is allowed to change. Thiele himself (1977) recognised the limitations of these data and quoted Lindroth (1949): "the very isolation of such (external) factors is an unnatural process". As stressed by Thiele (1977), it is irrelevant to study thermic preferences without taking into account the relative humidity. Nevertheless, results of such preference experiments were largely used to describe the habitat preferences of carabid beetles.

Another way to investigate the relationships between species and their habitat is to investigate in the field the presence or absence of species or their densities within different habitats. This approach has the advantage of taking into account simultaneously all the environmental variables potentially determining species habitat selection. Such a procedure was empirically used for instance by den Boer (1977) on the basis of his 'general field experience'. However, the development of multivariate statistical analysis provided a more objective tool to explore patterns relating species to their habitats. These methods allow the assessment of the relative influence of distribution factors determining specific habitat selection patterns at the community level; they are commonly applied to a wide range of animal and vegetation taxa (see e.g., Blondel 1986).

Only a few studies using multivariate analysis have been applied to carabid beetles. Carabid communities of 9 woodland associations in the region of Neuchâtel (Switzerland) were compared by correspondance analysis and classification (Borcard 1982). A classification method was used to compare carabid communities from upland grass and peat sites in northern England (Butterfield & Coulson 1983). Large data sets from England (Luff et al. 1989), Belgium (Dufrêne et al. 1990) and Europe (Eyre and Luff 1990) were analysed with the help of ordination and classification methods. Results were difficult to interpret because of (1) the lack of standardization in data collecting, which only allowed the use of presence/absence data, and (2) the lack of precision in the habitat typology. Moreover, data sets from England and Europe were analysed by a severely controversial method of ordination, the detrended correspondence analysis (see Hill 1979; Hill & Gauch 1980 for the presentation of the method and Wartenberg et al. 1987 and Jackson & Sommers 1991 for the critics). Buse (1988) also used the same inaccurate method to investigate the habitat selection of beetles in 7 adjacent habitats. All these studies focused mainly on habitat comparison on the basis of their carabid communities, without quantitative references to environmental variables. Baguette (1987) presented a preliminary analysis of the Belgian woodlands carabid fauna on partial data; Baguette & Gérard (1993) analysed the effects of spruce plantation on carabid beetles in Southern Belgium. In both cases, multivariate analysis of carabid communities was related to environmental factors by a correlation method.
Consequently, the purpose of the present study is (1) to detect habitat selection patterns of woodland carabid beetles from standarized samples and (2) to compare the relative influence of some environmental factors in habitat selection. This study differs from most others in that is compares the abundance of carabids in each of the 68 sampling sites; moreover, a common set of environmental factors was measured in each site.

Materials and methods

Study area and sampling sites

The study area is the 'Région Wallonne', southern Belgium. This administrative region (16000 km^2) shows a range of altitude (from less than 50 m to 694 m), temperature (mean annual temperature between 6.5 °C and 9.5 °C), rainfall (mean precipitation between 700 and 1400 mm/yr) and frost (55–120 days/yr). Phytogeographically, the study area is at the border of Atlantic and Continental domain. Phytosociologically, semi-natural woodlands (4800 km^2) have been classified by Noirfalise (1984) according to the Braun-Blanquet system. Sixty-eight deciduous woodland sites were selected in the area on the basis of (1) their floral composition according to Noirfalise's classification and (2) their geographical locality: sampling sites had to be widely dispersed in the study area.
Sampling site descriptions include measures of (1) soil water holding capacity, (2) soil trophic status, (3) light on the ground, (4) soil pH, (5) soil type, (6) canopy cover, (7) shrub layer cover, (8) field layer cover, (9) field layer richness and (10) alitude (Table 1). Soil water holding capacity, soil trophic status and light on the ground were assessed on the basis of the presence of characteristic plant species, whose occurrence is restricted to well defined local conditions. Ecologial width of characteristic plant species have been defined by Noirfalise & Dethioux (1970). The floristic composition of the vegetation was described in each site in terms of vegetal association according to Noirfalise (1984) and the CORINE biotope classification (CEC 1991).

Sampling methods

Carabid beetles were sampled using pitfall traps, which consisted of half plastic bottles 17 cm high 8.5 cm diameter partially filled with 5% formol and detergent. In each site, ten traps were placed 5 m apart in a row or in a circle, depending on the configuration of the trees. The traps were in operation from April to October 1986. Samples were collected monthly.

Table 1. Sampling site description. Wat.: soil water on an arbitraty scale from 2.4 (dry) to 4.8 (waterlogged). Tro: soil trophic status on an arbitratry scale from 1.1 (organic soil) to 3.8 (ion rich soil). Light: light on the ground on an arbitratry scale from 1.7 (lighter) to 2.9 (darker). pH: soil pH from 1 (pH 3.1 – pH 4) to 5 (pH 7.1 – pH 8). Soil: soil type. 1. Rendzinas. 2. Brown earths. 3. Podzols. 4. Gley soils. 5. Peats. Cov1: canopy cover. (5: 75–100%; 4: 50–74%; 3: 25–49%; 2: 5–25%; 1: < 5%). Cov2: shrub cover, same scale as Cov1. Cov3: field cover, same scale as Cov1. FlRich: number of vegetal species in the field layer (1: 0–2; 2: 3–4; 3: 5–8; 4: 9–16; 5: 17–31). Altitude in m

Site	Wat	Tro	Light	pH	Soil	Cov1	Cov2	Cov3	FlRich	Altitude
1.	3.7	2.9	2.6	4	4	5	2	3	3	160
2.	2.6	3	2	4	2	5	4	4	2	204
3.	2.8	3	2.4	5	2	5	2	5	3	275
4.	3.1	2.2	2.4	2	3	4	0	5	2	250
5.	3.1	2.2	2.4	2	3	4	5	4	3	295
6.	3.1	2.2	2.4	2	3	4	5	4	4	315
7.	2.9	1.5	2.3	2	2	4	5	4	4	320
8.	2.4	3.8	1.7	5	1	5	5	4	3	200
9.	3.1	1.8	2.6	2	2	5	2	2	2	290
10.	2.8	3	2.4	5	2	5	4	4	3	235
11.	3.2	2.6	2.5	2	3	5	5	5	3	275
12.	3.3	2.7	2.5	4	3	5	5	2	4	360
13.	4.8	1.1	2.3	1	5	5	0	5	2	590
14.	2.9	1.5	2.3	2	2	5	4	2	2	390
15.	2.9	2	2.5	2	2	5	5	2	2	400
16.	3.1	1.8	2.6	2	2	5	1	2	2	410
17.	3.7	2.9	2.6	4	4	5	3	5	3	380
18.	3.1	1.8	2.6	2	2	5	1	1	2	480
19.	4.8	1.1	2.3	1	5	5	0	5	2	635
20.	3.6	2.4	2.6	4	4	5	4	5	4	250
21.	3.1	1.8	2.6	2	2	4	0	3	4	455
22.	3.3	2.8	2.7	3	3	3	4	5	4	315
23.	3.8	1.5	2.8	2	5	5	4	5	3	360
24.	3.1	2	2.6	2	2	5	1	2	4	240
25.	3.7	2.9	2.6	4	4	3	2	5	5	230
26.	3.7	2	2.6	3	3	4	3	5	5	375
27.	4.8	1.1	2.3	1	5	5	0	5	2	350
28.	3.4	3	2.9	3	3	5	0	5	4	145
29.	2.8	3	2.4	5	2	5	0	5	3	155
30.	3.7	2	2.6	3	3	4	3	5	4	180
31.	3.2	2.9	2.6	3	3	3	3	5	4	170
32.	3	1.8	1.7	2	3	5	3	1	3	130
33.	3	1.8	1.7	2	3	5	3	5	4	140
34.	3.7	2.9	2.6	4	4	4	4	5	5	110
35.	2.6	3	2	4	2	0	5	2	3	170
36.	3.2	2.9	2.6	3	3	4	3	5	4	180
37.	3.1	2.2	2.4	2	3	5	5	2	4	235
38.	3.7	2.9	2.6	4	6	5	2	5	4	180
39.	3.3	2.7	2.5	4	3	5	1	5	4	195
40.	2.8	3	2.4	5	2	5	3	5	4	270
41.	3.4	3	2.9	3	3	5	5	5	4	250
42.	3.1	2.2	2.4	2	3	5	3	2	4	280
43.	3.7	2	2.6	3	3	3	5	5	4	215
44.	2.6	3	2	4	2	4	5	2	4	200
45.	2.6	3	2	4	2	5	5	5	4	190
46.	4.8	1.1	2.3	1	5	4	0	5	2	540
47.	3.1	1.8	2.6	2	2	5	2	4	2	420
48.	3.1	1.8	2.6	2	2	5	0	5	3	530
49.	3.7	2	2.6	3	3	5	3	5	4	340

Table 1. (Continued)

Site	Wat	Tro	Light	pH	Soil	Cov1	Cov2	Cov3	FlRich	Altitude
50.	3.4	3	2.9	3	3	1	2	5	4	310
51.	2.8	3	2.4	5	2	5	2	2	4	220
52.	2.9	1.5	2.3	2	2	5	2	5	3	360
53.	3	1.8	2.4	2	2	5	2	1	3	260
54.	3.4	3	2.9	3	3	5	5	4	3	290
55.	3.3	2.8	2.7	3	3	5	5	5	4	250
56.	4.8	1.1	2.3	1	5	5	0	5	2	430
57.	3.1	1.8	2.6	2	2	5	3	2	2	420
58.	2.9	1.5	2.3	2	2	5	3	3	1	370
59.	3	1.8	2.4	2	2	5	2	3	2	380
60.	3.1	1.8	2.6	2	2	5	5	2	4	240
61.	3.1	2.2	2.4	2	3	4	5	1	3	255
62.	3.2	2.6	2.5	2	3	5	5	4	2	165
63.	3.2	2.6	2.5	2	3	5	5	5	2	80
64.	3.2	2.6	2.5	2	3	5	5	5	2	85
65.	3.2	2.6	2.5	2	3	5	4	5	2	75
66.	4.4	3	2	5	4	0	5	5	4	60
67.	3.1	1.8	2.6	2	2	5	4	4	2	590
68.	4.7	1.5	2.4	2	4	4	2	5	3	360

Statistical analysis

Sampling site descriptors were analysed by principal component analysis (PCA). PCA axis 1, 2 and 3 were used as synthetic variables of environmental data. In the same way, the axis 1 and 2 of a correspondence analysis were used to summarize the floristic composition of each site. Carabid data were analysed by ordination (correspondence analysis) and classification methods. The CA (program ACOBI of Lebart et al. 1977) was used to describe the interactions between species and between samples, and to detect the main directions of covariability. Structure of carabid samples was compared by Kulczynski's index of similarity (Legendre & Legendre, 1984). The matrix of similarity between sites was submitted to the intermediate linkage with 75% connexity agglomerative clustering method (Legendre & Legendre, 1984). Dispersion ellipses (80% of probability) of the clusters were computed in the CA factorial space. The relationships between the carabid species' relative abundance and the synthetic variables of site descriptors or floristic composition were measured by multivariate canonical correspondence analysis (Jongmann et al. 1987; ter Braak 1988) and by rank correlations.

Results

The total sample includes 33208 carabid beetles belonging to 98 species (25% of the Belgian fauna: Desender 1985, 1987, 1990). For each species, Table 2 shows (1) the number of individuals recorded and (2) the number of sites where the species was collected.

Carabid communities ordination

Axes one, two, three and four of the correspondence analysis account respectively for 16.9, 14.6, 10.7 and 8.7% of the total variance. Waterlogged woodlands are separated from the others along axis one (Fig. 1a). Forests on peaty soil and woodlands of river banks are on the right, all the other sites are clumped near the origin. This axis corresponds to an opposition between species living in waterlogged woodlands, like *Loricera pilicornis*, *Patrobus atrorufus* or *Pterostichus strenuus*, and very common woodland dwellers avoiding waterlogged sites, like *Abax parallelepipedus*, *Pterostichus madidus* and *P. oblongopunctatus*

Table 2. Number of individuals recorded and number of sites per carabid species

Species	Individuals	Sites	Species	Individuals	Sites
Abax ovalis	1187	30	*Carabus violaceus*	93	12
Abax parallelus	714	43	*Chlaenius nigricornis*	3	3
Abax parallelepidedus	9534	63	*Chlaenius nitidulus*	4	1
Agonum assimile	1656	35	*Clivina collaris*	3	2
Agonum dorsale	2	1	*Clivina fossor*	22	5
Agonum fuliginosum	137	7	*Cychrus attenuatus*	354	24
Agonum gracile	2	2	*Cychrus caraboides*	113	24
Agonum livens	28	4	*Dyschirius globosus*	44	5
Agonum marginatum	1	1	*Elaphrus cupreus*	17	5
Agonum micans	6	3	*Harpalus aeneus*	5.1	3
Agonum moestum	25	5	*Harpalus atratus*	3	2
Agonum muelleri	45	6	*Harpalus distengendus*	1	1
Agonum obscurum	30	7	*Harpalus latus*	11	5
Agonum ruficornis	1	1	*Harpalus rufibarbis*	1	1
Agonum viduum	3	2	*Leistus fulvibaris*	1	1
Agonum viridicupreum	1	1	*Leistus piceus*	8	7
Amara communis	8	5	*Leistus rufomarginatus*	4	2
Amara convexior	4	3	*Leistus rufescens*	4	4
Amara familaris	6	4	*Licinus hoffmannseggi*	1	1
Amara lunicollis	6	4	*Loricera pilicornis*	198	24
Amara ovata	11	3	*Molops piceus*	465	33
Amara plebeja	8	4	*Nebria brevicollis*	108	37
Amara similata	28	8	*Nebria salina*	4	2
Asaphidion flavipes	15	4	*Notiophilus biguttatus*	71	16
Badister bipustulatus	28	9	*Notiophilus palustris*	1	1
Badister lacterosus	3	1	*Panageus crux-major*	2	1
Badister sodalis	6	2	*Patrobus atrorufus*	286	6
Bembidion biguttatum	3	2	*Pterostichus anthracinus*	6	4
Bembidion bruxellense	13	1	*Pterostichus cristatus*	1168	41
Bembidion dentellum	3	1	*Pterostichus cupreus*	48	19
Bembidion guttula	52	1	*Pterostichus diligens*	76	7
Bembidion lampros	19	5	*Pterostichus madidus*	4376	62
Bembidion obtusum	2	1	*Pterostichus melanarius*	91	10
Bembidion properans	154	10	*Pterostichus minor*	80	7
Bembidion tetracolum	188	4	*Pterostichus nigrita*	505	22
Bembidion tibiale	2	2	*Pterostichus niger*	211	21
Bembidion unicolor	1	1	*Pterostichus oblongopunctatus*	7725	61
Calathus fuscipes	2	1	*Pterostichus rhaeticus*	409	12
Calathus melanocephalus	1	1	*Pterostichus strenuus*	89	15
Calathus piceus	2	2	*Pterostichus vernalis*	47	6
Calosoma inquisitor	45	5	*Pterostichus versicolor*	4	3
Carabus arvensis	22	7	*Stomis pumicatus*	1	1
Carabus auratus	14	4	*Trechus obtusus*	4	4
Carabus auronitens	281	25	*Trechus quadristratus*	1	1
Carabus coriaceus	81	24	*Trechus rivularis*	32	4
Carabus granulatus	91	8	*Trechus secalis*	72	6
Carabus monilis	4	3	*Trichotichnus laevicollis*	105	22
Carabus nemoralis	524	41	*Trichotichnus nitens*	89	12
Carabus problematicus	1870	49	*Trichocellus placidus*	1	1

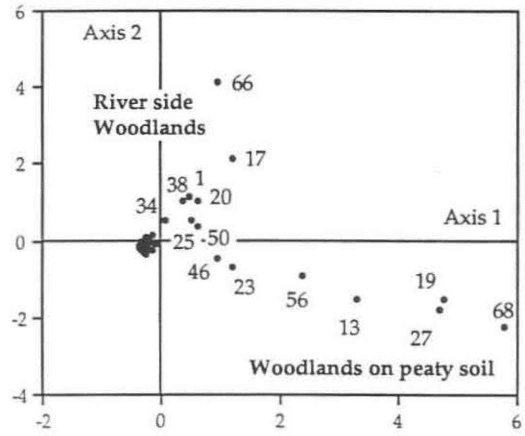

Fig. 1a. Projection of the 68 sampling sites in the factorial space of the CA axes 1–2. Only sites with a score higher than 1% are identified

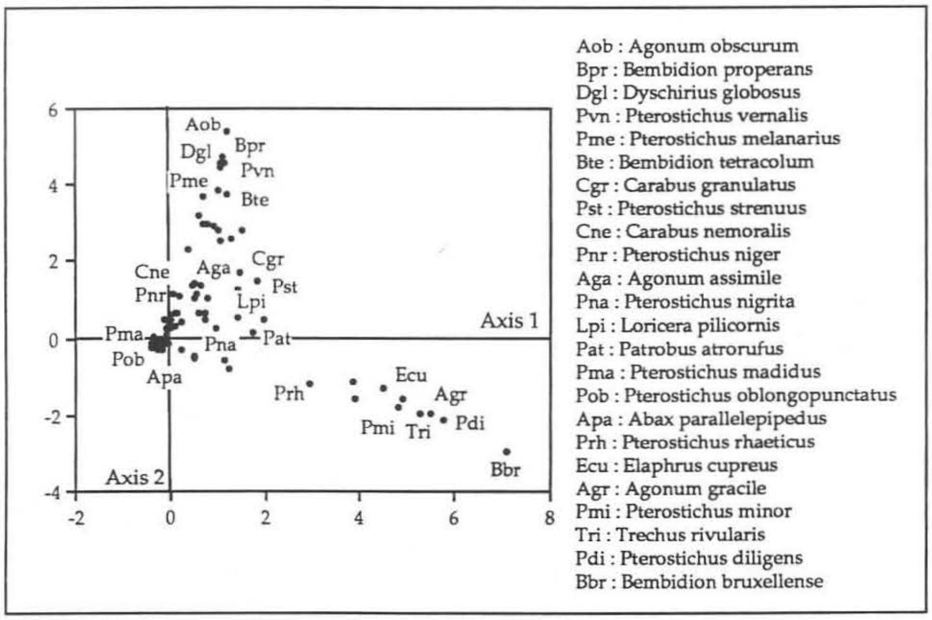

Fig. 1b. Projection of the 98 carabid species in the factorial space of the CA axes 1–2. Only species with a score higher than 1% are identified

(Fig. 1b). Axis two (Fig. 1a) segregates woodlands of river banks at the top from woodlands on peaty soil at the bottom. Specialists of woodlands on peaty soil are *Agonum gracile*, *Bembidion bruxellense*, *Elaphrus cupreus*, *Pterostichus diligens*, *P. minor*, *P. rhaeticus* and *Trechus rivularis*; species of river banks woodlands are *Agonum obscurum*, *Bembidion properans*, *B. tetracolum*, *Carabus granulatus*, *Dyschirius globosus*, *Pterostichus melanarius*, *P. strenuus* and *P. vernalis* (Fig. 1b). Some species living both in woodlands of river banks and in dryer woodlands also have a high score on axis two: *Agonum assimile*, *Carabus nemoralis*, *Pterostichus niger* and *P. nigrita*. The heterogeneity between woodlands of river

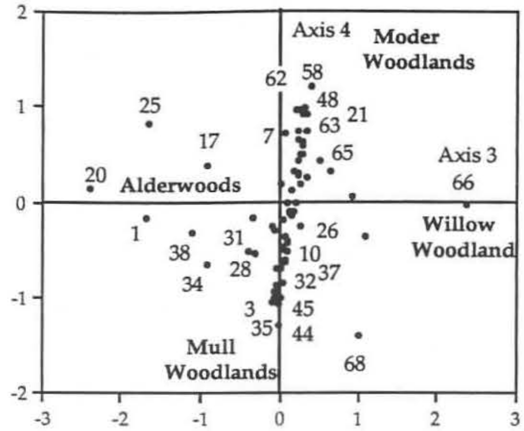

Fig. 2a. Projection of the 68 sampling sites in the factorial space of the CA axes 3–4. Only sites with a score higher than 1% are identified

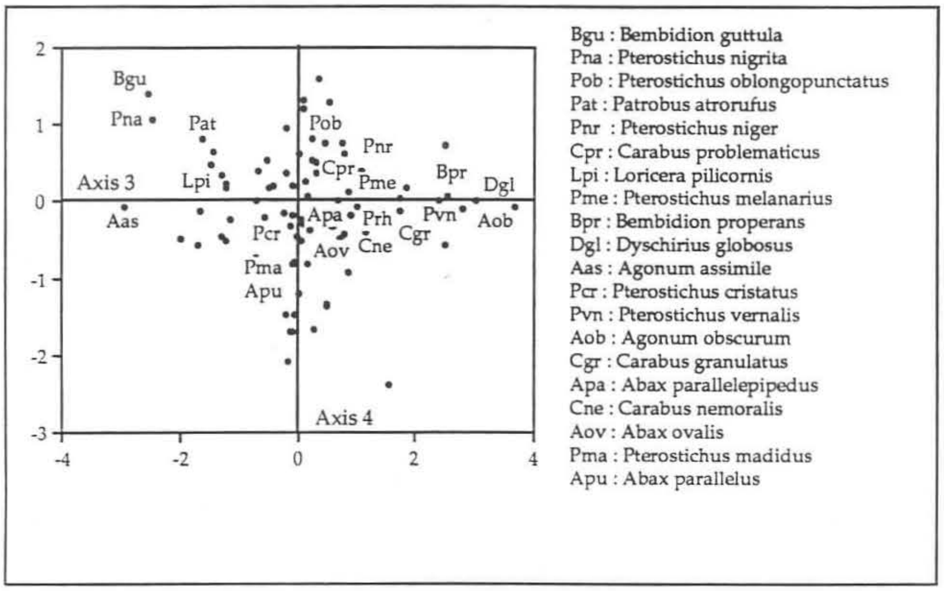

Fig. 2b. Projection of the 98 carabid species in the factorial space of the CA axes 3–4. Only species with a score higher than 1% are identified

banks is shown along axis three: alderwoods (*Stellario-Alnetum*) on the left are separated from the willow woodland (*Salicetum*) on the right (Fig. 2a). Species dwelling in alderwoods are *Agonum assimile*, *Bembidion guttula*, *Loricera pilicornis*, *Patrobus atrorufus* and *Pterostichus nigrita*; species of the willow woodland are *Agonum obscurum*, *Bembidion properans*, *Carabus granulatus*, *Dyschirius globosus*, *Pterostichus melanarius*, and *P. vernalis*. Axis four segregates acid soil woodlands with a thick, moder or dysmoder, humus on the top from chalk woodlands with a thin, mull humus on the bottom (Fig. 2a). Characteristic species of chalk woodlands are *Abax ovalis*, *A. parallelus*, *Carabus nemoralis* and *Pterostichus madidus* and to a lesser extent *Abax parallelepipedus*, *Agonum assimile* and *Pterostichus*

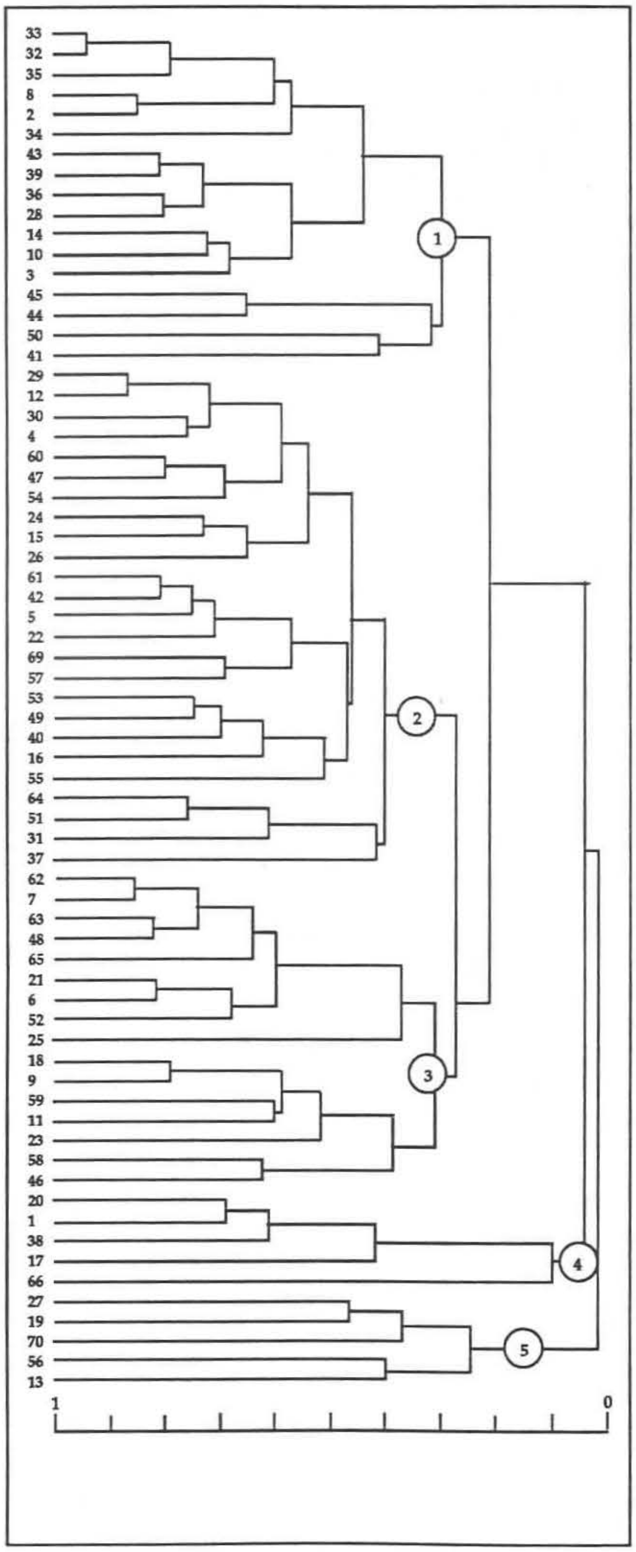

Fig. 3. Dendrogramm of the 68 sites classified on the basis of their carabid communites

cristatus. Specialists of acid soil woodlands are *Carabus problematicus*, *Pterostichus oblongopunctatus* and *P. niger* (Fig. 2b). The differential abundance of *Pterostichus madidus* and *P. oblongopunctatus* in these two kinds of woodlands is the main reason for the opposition of these two groups.

Carabid communities classification

Results are shown as a dendrogram in Fig. 3. The 68 sites are organised into 5 clusters: (1) 17 sites with high abundance of *Abax ovalis*, *Carabus nemoralis* and *Pterostichus madidus* and low abundance of *Carabus problematicus* and *Pterostichus oblongopunctatus*, (2) 25 sites where the abundance of these 5 species are more or less similar, (3) 16 sites with high abundance of *Carabus problematicus* and *Pterostichus oblongopunctatus* and low abundance of *Abax ovalis*, *Carabus nemoralis* and *Pterostichus madidus*, (4) all but two woodlands on river banks and (5) all but two woodlands on peaty soil. Dispersion ellipses of these 5 groups in the axes 1−2 and 1−4 spaces of the correspondence analysis are shown at Fig. 4. Community classification is in good agreement with community ordination.

Distribution and environmental factors

Relationships between carabid data and synthetic environmental variables (PCA axis 1−3 on the site descriptor matrix and CA axis 1 and 2 of the floristic data matrix) were investigated by canonical correspondance analysis. The total inertia of the carabid data was decomposed in fractions explained by site descriptors, floristic composition or both, following the procedure of ter Braak (1990). Results (Table 3) show that only 27% of the carabid data information remains unexplained; moreover, we detect an unexpected effect of the vegetation in the description of carabid distribution: more that 50% of the carabid data information is common with the floristic data matrix.
Rank correlations between sites coordinates on the four axes of the carabid CA and (1) the two axes of the floristic data and (2) site descriptors are shown at Table 4. Ordination on the two axes of the Ca on floristic data ist strongly related to the axes one and two

Table 3. Proportion of the total variance of the carabid data matrix explained by synthetic environmental and floristic variables

Source of variation	Proportion
Effect of both environmental and floristic variables	30.4%
Effect of floristic variables only	23.1%
Effect of environmental variables only	19.3%

Table 4. Spearman rank correlations between (1) the coordinates of the sampling plots on the axes 1, 2, 3 and 4 of the CA on the carabid data and (2) the sampling site descriptors. N = 68. *: $p < 0.05$. **: $p < 0.01$. Wat.: soil water. Tro: soil trophic status. Light: light on the ground. pH: soil pH. Soil: soil type. Cov1: canopy cover. Cov2: shrub cover. Cov3: field cover. FlRich: number of vegetal species in the field layer. Alt: Altitude

Axis	Wat	Tro	Light	pH	Soil	Cov1	Cov2	Cov3	FlRich	Alt
A1	0.614**	−0.205*	0.158	−0.154	0.553**	−0.117	−0.185	0.433**	−0.140	0.282**
A2	−0.084	0.658**	0.142	0.696**	0.080	−0.189	0.322**	0.066	0.449**	0.455**
A3	0.091	−0.627**	−0.182	−0.661**	0.040	0.073	−0.162	−0.148	−0.506**	0.447**
A4	0.167	−0.317**	0.229*	−0.414**	0.020	0.071	−0.109	−0.010	−0.337**	0.371**

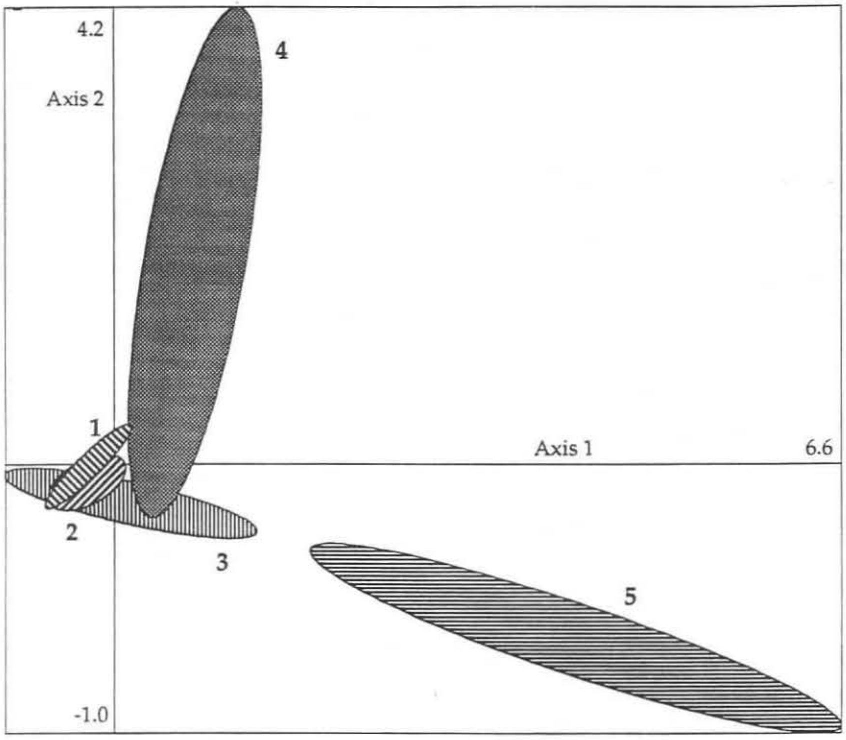

Fig. 4a. Dispersion ellipses (80% of probability) of the 5 groups isolated by the classification in the factorial space of the CA axes 1–2

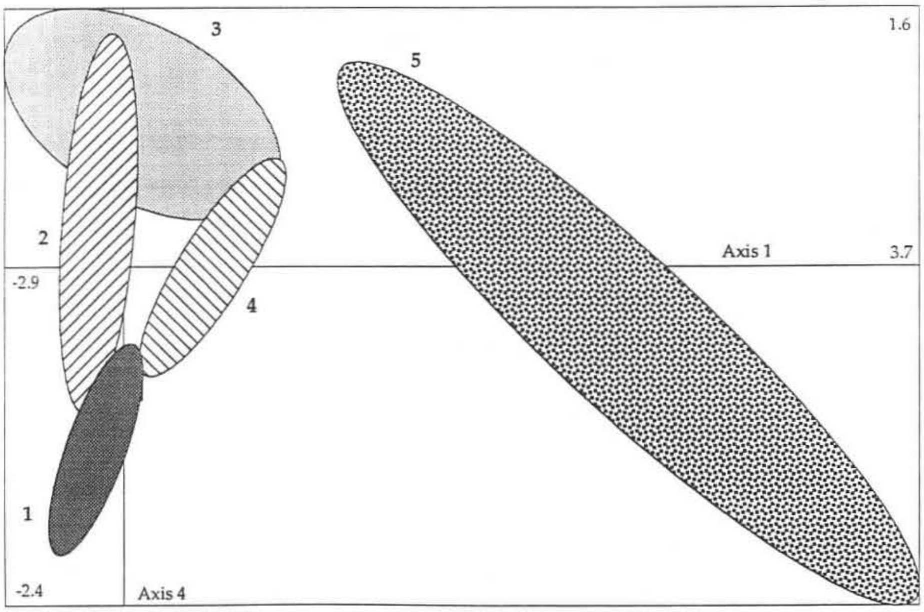

Fig. 4b. Dispersion ellipses (80% of probability) of the 5 groups isolated by the classification in the factorial space of the CA axes 1–4

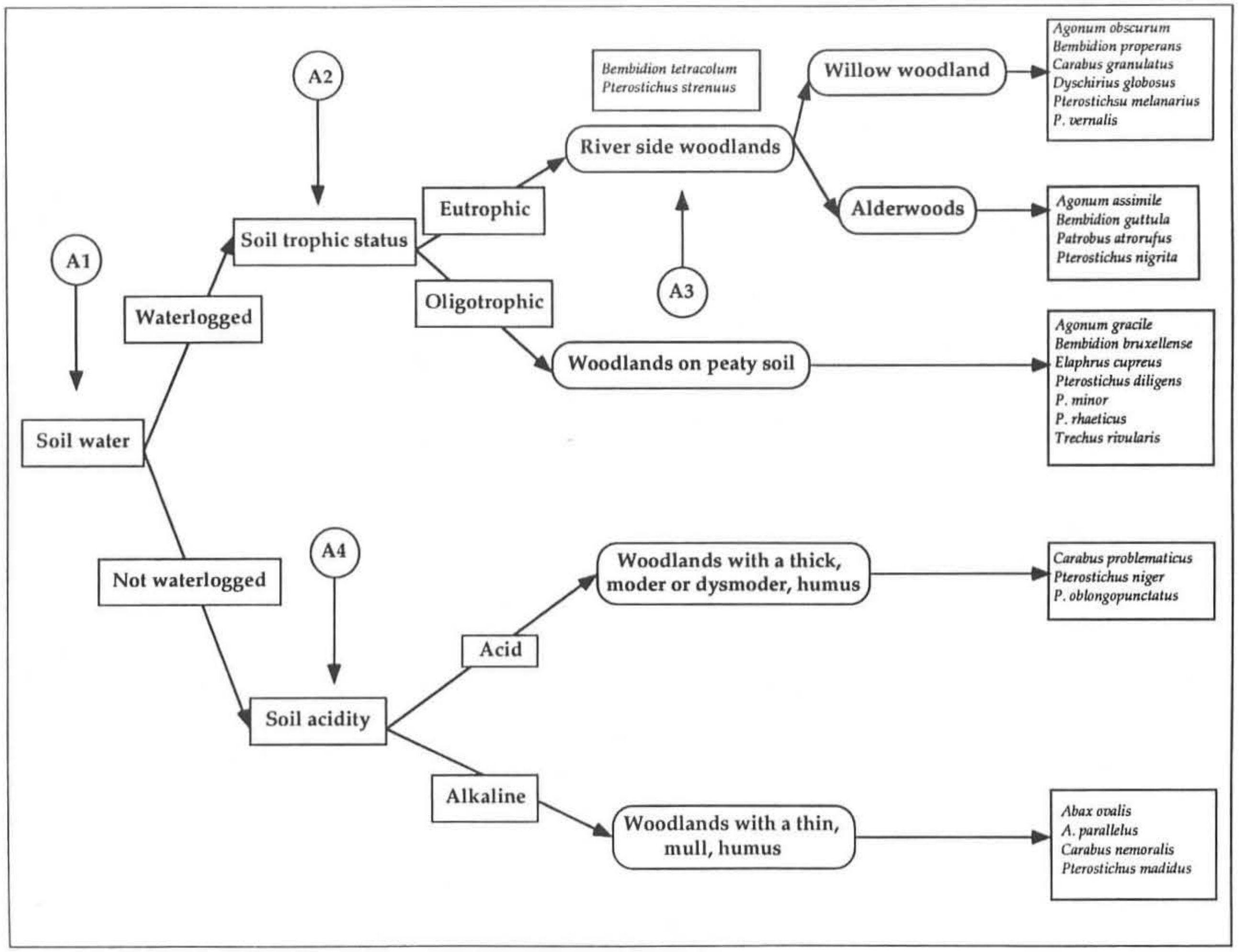

Fig. 5. Habitat selection sequence of woodland carabids. A1, 2, 3, 4: selection according to the axis 1, 2, 3, 4 of the CA

of the carabid CA. Ordination of carabid communities on the first CA axis is strongly related to (1) soil water content, (2) soil type, (3) field layer cover and (4) altitude and to a lesser extent to soil trophic status. These correlations emphazise the particularity of waterlogged woodland carabid communities. Ordination on the second CA axis is strongly correlated with (1) soil acidity, (2) soil trophic status, (3) altitude, (4) floristic species richness of the field layer and (5) shrub layer cover. These factors explain the habitat segregation between hygrophilic species living in (1) mesotrophic or eutrophic woodlands of river banks of lowland and (2) oligotrophic highland woodlands on peaty soils. Ordination on the third CA axis is related to (1) soil acidity, (2) soil trophic status, (3) floristic species richness of the field layer and (4) altitude. These variables explain the separation of the willow woodland community from alderwood communities. Ordination on the fourth CA axis is correlated with (1) soil acidity, (2) soil trophic status, (3) floristic species richness of the field layer and (4) altitude. Two species show a high score on this axis: *Pterostichus madidus* and *P. oblongopunctatus*. Habitat selection sequence of the woodland fauna brought out be the combination of correspondence analysis and correlation with ecologial variables is shown in Fig. 5.

Discussion

'It is not to be expected that a particular (carabid) species to be found exclusively in any one plant community' (Thiele 1977). The present large scale inventory of deciduous woodland communities confirms this view. Sufficiently abundant carabid species are almost never restricted to one distinct woodland community. However, phytosociology appears to be useful to provide a reference for habitat description and typology. The variation of carabid abundance in different plant communities can be related to the variation of environmental variables underlying the presence of particular plant combinations. A standarized phytosociological typology, like the CORINE biotope manual (CEC 1991) should be useful in the future to increase the accuracy of habitat selection description of carabid beetles.

The procedure used in the present study allows (1) the discrimination and (2) the hierarchisation of distribution factors at the community level. Specific requirement data presented here concern only species with a high discriminant power towards these factors. Other multivariate methods should give the individual species' response to each environmental variable. Rushton et al. (1990) developed an elegant combination of reciprocal averaging ordination and logistic regression to test the relationship between species presence along an environmental gradient. The habitat selection pattern of each carabid species could be obtained by this method.

Soil water and altitude were already identified by Eyre and Luff (1990) as important factors in the distribution of carabid species. This was postulated only on the basis of the relative position of the sites in their ordination. The present study confirms the importance of soil water holding capacity. The contribution of altitude should be viewed more cautiously. It is well known that at regional scale, climatic and edaphic variables are always related to altitude. Such environmental variables with an indirect effect on the distribution should be distinguished from others directly related to prey availability or ecophysiological requirements, like all the other ecologial variables investigated in the present study. It is always possible to find synthetic variables more or less determining the extent of ecological factor variations to which species are sensitive. Such synthetic variables like altitude or space position (see the so-called 'new paradigm' of spatial autocorrelation, Legendre 1993) are of course interesting in the description of species distribution; however, these variables should never be used as explanations of species habitat selection patterns. This emphazises the need of an experimental approach focusing on causal explanations of the distribution. Nevertheless, some causal relations between carabid distribution and their feeding ecology emerge from the present analysis. The strong opposition between habitat

preferences of *Pterostichus madidus* and *P. oblongopunctatus* may be related to a difference in prey availability: *P. madidus* feeds mainly on earthworms (Luff 1974), while *P. oblongopunctatus* feeds on insects living in humus like springtails (Penney 1967), larvae of the Trichoptera *Enoicycla pusilla* (Loreau 1983) and Diptera Nematocera (Penney 1967; Loreau 1983). The availability of these two groups of prey depends mainly on the humus type: earthworms are more abundant in mull humus, while insects are characteristic of moder or dysmoder humus. However, informations on the natural food of carabids are too incomplete to explain the ecological requirements of each species (Hengeveld 1980a). Plant remains were found into the digestive track of each of the 24 carabid species investigated by Hengeveld (1980b). Hence, relations between carabid and plant distribution are probably stronger than a common reaction to environmental factors and must be related to carabid feeding ecology. Most species are predators feeding on phytophagous organisms, themselves more or less related to a particular vegetation. Here again, the introduction of a careful experimental approach should be useful to detect species by species the precise influence of the food availability as a causal explanation of habitat selection.

Conclusions

The present study introduces an objective methodology (1) to identify and (2) to asses the hierarchy of the distribution factors determining carabid beetles' habitat selection at the community level. Its development within the framework of carabidology should increase the detection of habitat selection patterns at the regional scale. Moreover, this study reveals the lack of basic knowledge of the biology of most carabids. Its suggests fruitful studies that might elucidate the processes producing patterns of habitat selection at the regional scale.

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